FINAL REPORT

For: Vertebrate Pest Control Research Advisory Committee

STUDY TITLE:

Rangeland forage loss from California ground squirrels

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August 2021

ABSTRACT

California ground squirrels (*Otospermophilus* spp.) cause more economic damage to California rangelands than any other rodent. Damage comes in many forms, although forage loss is typically the greatest concern. These losses are believed to be significant for ranchers, particularly given the economically marginal environment that they exist in, yet our understanding of these economic losses is limited. Furthermore, current public opinion is often not supportive toward ground squirrel control on many public grazing lands. Information on the damage that ground squirrels cause to rangelands may be needed to justify management actions in the future. Therefore, we evaluated the amount of standing crop removed by California ground squirrels across 16 sites at four different ground squirrel density categories in central California rangelands from 2019 through 2020. We also included precipitation and livestock grazing intensity to help account for their potential effect on forage production. We found that ground squirrel abundance negatively affected standing crop biomass, with available forage reduced by 27.2 kg ha^{-1} at the end of the growing season per individual ground squirrel. Likewise, precipitation influenced standing crop, with each cm of precipitation yielding a 16.6 kg ha^{-1} increase in available forage. We did not observe any effect of livestock grazing intensity, an interaction between livestock grazing intensity and ground squirrel abundance, nor an interaction between precipitation and ground squirrel abundance on residual standing crop. Collectively, this information will be useful to ranchers to help determine when control efforts may be needed for California ground squirrels given relative abundance of ground squirrels on their rangeland properties.

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INTRODUCTION

California ground squirrels (*Otospermophilus douglasii, Otospermophilus beecheyi*) are common rodent species found from southern Washington to northern Mexico (Koprowski et al., 2016). California ground squirrels have been identified as the most damaging rodent species in California rangelands (8.4% loss in revenue to ranching operations, Baldwin et al., 2014), and hence are considered a pest species. Common examples of damage caused by ground squirrels include herbaceous forage removal that lowers potential livestock production; the creation of burrow systems which pose a substantial risk to livestock health, piping of water (when water flows through burrows systems causing them to collapse) and subsequent erosion due to large-scale burrow systems; and damage to pond dams, roads, and other ranch infrastructure (Marsh, 1998; Baldwin et al., 2014; Quinn et al., 2018). Ranchers in general operate in an economically marginal environment, with many ranching families dependent on off-ranch jobs to help sustain the livestock operation (Brunson and Huntsinger, 2008). As such, damage caused by ground squirrels could have a substantial effect on ranch families. Ranchers need more information about the damage caused by ground squirrels to help determine when active management is justified to increase ranch profitability.

Quantitative information about ground squirrel impacts to ranching operations is also of interest to public land management agencies, as they often have lands that are managed through livestock grazing (Huntsinger et al., 2007). However, agency staff may have a limited understanding of day-to-day ranch operations and the economics of livestock production. One way to improve understanding between agencies and their lessees is to increase agency awareness of ranching operations such as pest management. Currently, land management agencies often do not allow control of some ground squirrel species (e.g., California ground squirrels; Wolf et al., 2017), but with a better understanding of the financial burden imposed by ground squirrels, some agencies may consider developing strategies to reduce ground squirrel-related costs to ranchers. Alternatively, these agencies could include reduced lease fees based on density of ground squirrels, or they could provide compensation for ranchers at sites that have ground squirrels in particularly high concentrations. It bears noting that conservation organizations, state and federal agencies, and other interested public groups have expressed concern about the use of anticoagulant rodenticides for managing field rodents due to potential negative effects to the ecosystem, further demonstrating that there is interest in how ground squirrels are managed on rangelands by individuals not directly tied to the ranching community (e.g., Rattner et al., 2014; Hindmarch and Elliott, 2018; Baldwin et al., 2021a). Data as to the level of damage caused by ground squirrels may be needed to further justify ground squirrel management in annual rangeland areas in the future.

To date, a minimal amount of research, mostly in the early- to mid-1900s, has been conducted to understand the costs of California ground squirrels to ranching operations. Over 60 years ago, Howard et al. (1959) investigated the impact of ground squirrels on livestock gains at the San Joaquin Experimental Range in the Sierra foothills. They found that weight gain increased 15 kg per heifer for 10 heifers in a single field where ground squirrels were eliminated compared to a field where ground squirrels were not eradicated. Previously, Fitch and Bentley (1949) determined that 6 male ground squirrels decreased the potential forage yield by 240 kg over a 0.2 ha enclosure. This amount was >10 times what they could consume over the given study period, clearly illustrating that forage loss is far more than just those food items consumed by ground squirrels. Even earlier, Grinnell and Dixon (1918) calculated that 200 ground squirrels consumed the same amount of forage as one steer, although this is likely an underestimate of forage loss from ground squirrels given that this assessment did not account for forage that was removed but not consumed. Regardless, all of these studies are very dated (62–103 years). A more recent and thorough investigation is needed to better account for variability in plant and rodent composition encountered throughout differing rangeland landscapes, as well as potential changes in landscape composition, use patterns, and climatic conditions over time. For example, forecasts for drier climates suggest a reduction in plant cover, height, and productivity over the next several decades (Lipiec et al., 2013; Larsen et al., 2014; Zhang et al., 2020; Liu et al., 2022), potentially increasing forage competition between livestock and wildlife (Marsh, 1998). Likewise, altering livestock grazing intensity can greatly influence rangeland plant composition and forage production, ultimately altering rodent composition, abundance, and subsequent rodent damage to grasslands (Li et al., 2011; 2016; Schieltz and Rubenstein, 2016; Wolf et al., 2018). These factors should be considered in concert with ground squirrel abundance to better define their potential impact on available forage for livestock. Therefore, our primary objective for this study was to identify a reduction in standing crop biomass caused by varying densities of California ground squirrels across multiple regions in central California. We also considered how precipitation and livestock grazing intensity could further affect residual standing crop to better define how ground squirrels affect forage availability. This study will provide baseline data on the impact that ground squirrels have on residual forage at the end of the growing season that ranchers and land managers can use to make informed decisions on when financial expenditures should be targeted toward ground squirrel management.

STUDY AREA

This study was conducted in rangelands in the interior and coastal foothill regions of central California, USA (Fig. 1). This portion of California is defined by a Mediterranean climate with cool, wet winters and hot, dry summers. Primary vegetative growth occurs on central California rangelands from November through May. Precipitation varied extensively across sites and years, with the growing season of 2018–2019 substantially wetter (range = 31.1–78.8 cm) than 2019–2020 (range = 16.7–46.7 cm) (Table 1). Dominant plant species varied across sites, but was primarily non-native annual grasses such as *Bromus hordeaceus*, *Avena fatua*, *Bromus rubens*, and *Festuca (Vulpia)* spp., as well as non-native annual forbs including *Erodium* spp., *Medicago* spp., *Trifolium* spp., and *Vicia sativa* (Table 1). All study sites were grazed by cattle at some point during the study, although grazing intensity varied substantially across sites (Table 1). Various grazing and browsing wildlife species could be found at these rangeland sites including mule deer (*Odocoileus hemionus*), Tule elk (*Cervus canadensis nannodes*), wild pigs (*Sus scrofa*), desert cottontails (*Sylvilagus audubonii*), black-tailed jackrabbits (*Lepus californicus*), California voles (*Microtus californicus*), western harvest mice (*Reithrodontomys magalotis*), and deer mice (*Peromyscus* spp.).

MATERIALS AND METHODS

Plot establishment

In 2019, we identified 12 ranches with variable ground squirrel activity for our study (Fig. 1; Sites 1–12). We used the majority of these ranches again in 2020, although we replaced Site 12 with Site 13 given that Site 12 no longer was available to us. We also excluded Site 8 in 2020

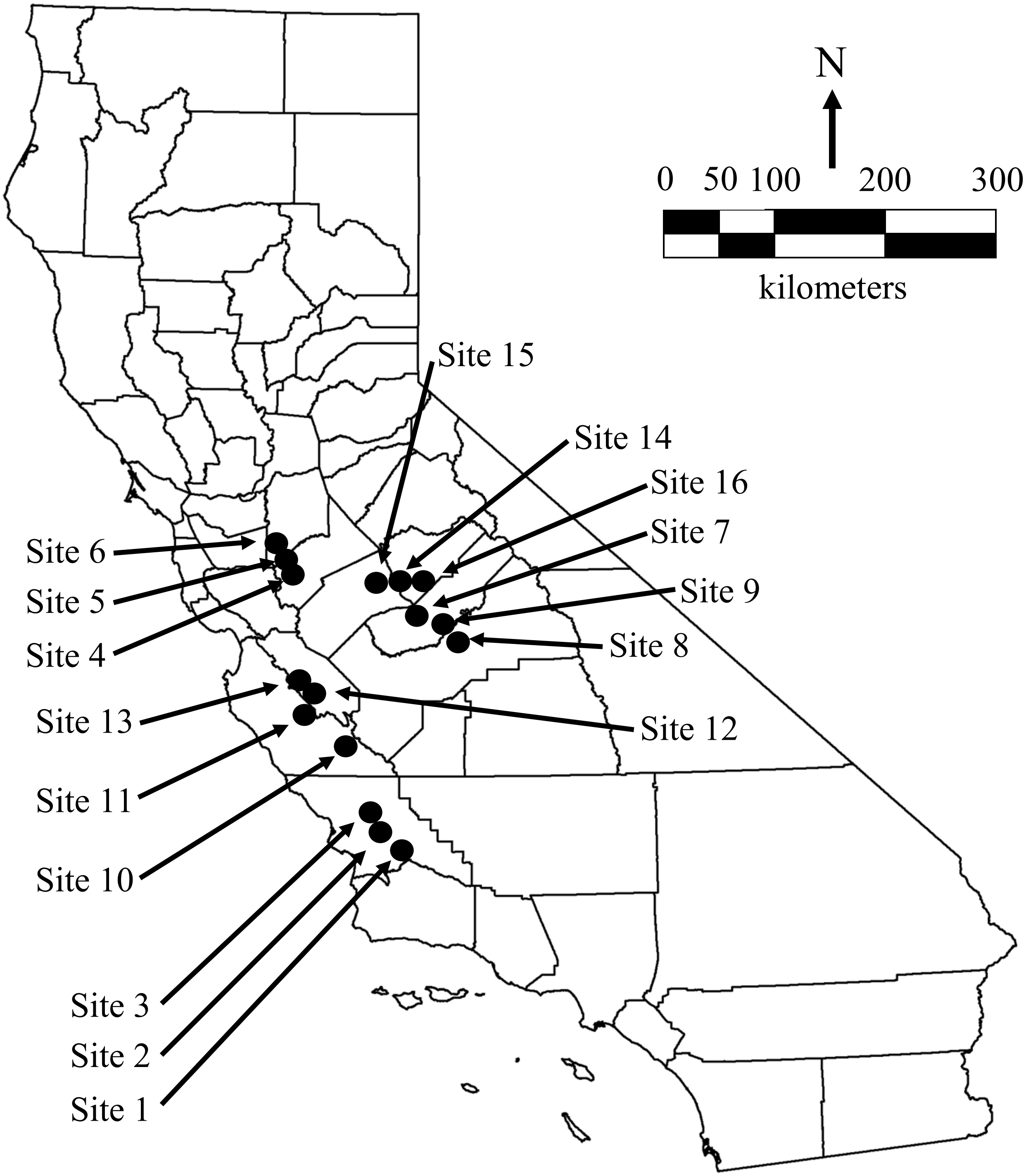

Figure 1. Location of rangeland field sites in central California, USA, during spring 2019 and 2020.

Table 1. The amount of precipitation (Precip) recorded during the forage production season, the number of Animal Unit Months (AUM), the maximum number of ground squirrels (GS) counted on study plots, and the standing crop (SC) biomass produced per study plot across all sites and years of this project. The most common grasses and forbs observed at each site are also included. All sites were located in rangelands in the central portion of California.

Site	Year	Precip (cm)	AUM ha^{-1}	GS count	SC (kg ha^{-1})	Common grasses	Common forbs
1	2019	78.8	0.91	0	1679	*Bromus hordeaceus*	*Erodium* spp.
			0.96	4	1081	*Festuca* spp.	*Medicago polymorpha*
			0.96	12	1065		
			0.96	19	822		
	2020	40.2	0.89	0	2467		
			0.95	3	1548		
			0.95	14	1197		
			0.95	19	762		
2	2019	31.1	1.3	1	1394	*Bromus rubens*	*Erodium* spp.
			0.8	4	1200	*Festuca* spp.	
			0.8	12	1032	*Bromus hordeaceus*	
			0.8	24	482		
	2020	24.8	1.3	0	853		
			0.8	5	1239		
			0.8	14	980		
			0.8	19	1182		
3	2019	31.1	7.16	0	1359	*Bromus rubens*	*Erodium* spp.
			7.16	5	1325	*Festuca* spp.	
			7.16	10	864	*Bromus hordeaceus*	
			7.16	16	1179		
	2020	24.8	7.2	0	1079		

			7.2	4	1509		
			7.2	14	1048		
			7.2	17	800		
4	2019	49.1	1.17	0	1363	*Hordeum murinum*	*Erodium* spp.
			2.01	7	1509	*Bromus hordeaceus*	
			2.16	17	768	*Bromus rubens*	
			2.01	30	1043		
	2020	16.7	1.13	0	496		
			2.08	6	267		
			2.08	9	247		
			2.08	22	232		
5	2019	49.1	1.63	0	2244	*Hordeum murinum*	*Medicago polymorpha*
			4.83	6	2778	*Bromus madritensis*	*Erodium* spp.
			4.83	10	2484	*Avena fatua*	
			4.83	16	2134		
	2020	16.7	1.63	0	684		
			4.83	5	1030		
			4.83	10	727		
			4.83	19	311		
6	2019	49.1	1.54	0	2612	*Avena fatua*	*Erodium* spp.
			1.54	6	2672	*Bromus diandrus*	
			1.54	15	2112	*Bromus hordeaceus*	
			1.49	23	2336		
	2020	16.7	1.35	0	1865		
			1.35	7	1420		
			1.35	12	1138		
			1.35	19	1367		
7	2019	60.5	9.67	1	907	*Bromus hordeaceus*	*Erodium* spp.
			9.67	5	800	*Vulpia myuros*	*Trifolium* spp.

			9.67	9	757		
			9.67	19	658		
	2020	30	8.77	0	1121		
			8.77	5	811		
			8.77	15	1069		
			8.77	17	868		
8	2019	60.5	1.08	1	812	*Bromus hordeaceus*	*Erodium* spp.
			1.08	6	942	*Vulpia myuros*	*Amsinckia* spp.
			1.08	14	879	*Bromus diandrus*	
			1.08	19	578		
9	2019	60.5		1	1277	*Bromus hordeaceus*	*Erodium* spp.
				4	821	*Bromus diandrus*	*Amsinckia* spp.
				10	458	*Hordeum murinum*	
				18	902		
	2020	30		0	1388		
				4	785		
				10	618		
				17	436		
10	2019	31.8		0	2046	*Bromus hordeaceus*	*Erodium* spp.
				5	1814	*Avena* spp.	*Vicia* spp.
				12	1324	*Festuca* spp.	
				14	736		
	2020	25.4		0	1954		
				2	2099		
				5	1834		
				11	2350		
11	2019	44.6	2.06	1	3492	*Hordeum murinum*	*Erodium* spp.
			3.24	5	2348	*Bromus hordeaceus*	*Hirschfeldia incana*
			3.24	7	3119	*Bromus diandrus*	

			2.99	10	1430		
	2020	29.9	1.32	0	2675		
			1.19	7	938		
			1.19	8	1928		
			1.13	15	981		
12	2019	46.5	0.37	2	400	*Bromus hordeaceus*	*Erodium* spp.
			0.37	4	973	*Festuca* spp.	*Croton setiger*
			0.37	8	870	*Bromus madritensis*	*Trichostema lanceolatum*
			0.37	11	415		
13	2020	29.9	10.53	0	792	*Hordeum murinum*	*Erodium* spp.
			10.53	3	1248	*Bromus hordeaceus*	*Hirschfeldia incana*
			10.53	6	1149	*Festuca* spp.	*Medicago polymorpha*
			3.08	13	1401		
14	2020	30.9	1.83	0	1918	*Bromus hordeaceus*	*Erodium* spp.
			1.83	7	1263	*Avena fatua*	*Datura* spp.
			1.83	8	1462	*Cynodon dactylon*	*Medicago* spp.
			1.83	14	1160		*Trifolium* spp.
15	2020	30.9	4.81	0	1559	*Avena fatua*	*Erodium* spp.
			4.81	4	1269	*Bromus hordeaceus*	*Medicago* spp.
			4.81	7	1172		*Trifolium* spp.
			4.81	10	1124		
16	2020	46.7	3.91	1	1411	*Bromus hordeaceus*	*Erodium* spp.
			3.91	5	1224	*Avena fatua*	*Amsinckia* spp.
			3.91	9	1397		
			3.91	13	1232		

due to a lack of access from Covid-19 restrictions. We added 3 additional sites in 2020 to bolster our sampling effort (Sites 14–16).

At each site, we initially scouted ground squirrel activity to identify 0.4 ha square plots (64 × 64 m) that exhibited a range of ground squirrel densities. Our target for ground squirrel abundance within a given plot included four categories: minimal (0–1 ground squirrels), low (2–6 ground squirrels), moderate (7–15 ground squirrels), and high (>15 ground squirrels). We selected these categories to represent the gradient of densities of California ground squirrels that are commonly found in rangelands in the western U.S. We also looked for sites with minimal slopes to reduce the potential impact that slope and aspect might have on forage production, and all sites were located >100 m from each other to help maintain independence ($\bar{x}$ diameter of home range = 20–34 m; Boellstorff and Owings, 1995). Once plot locations were identified, the perimeter of the plots were marked with wire flags to outline the observation area for visual counts.

Visual counts

We used the visual count method outlined by Baldwin et al. (2021b) to assess ground squirrel abundance within the study plots. In summary, an observation point was established outside the study plot. An observer generally parked a vehicle at the site to use it as a blind. If the observer could not use the vehicle as a blind, they identified an elevated location outside the plot to conduct counts. The observer waited 10 to 15 minutes after arrival at the site to initiate counts. For counts, the observer used binoculars to scan the entire study plot and counted all ground squirrels that were observed during this scan, being careful not to double count squirrels during the same scan. A total of 5 scans were made during each visual count period, with initiation of subsequent scans separated by 5 minutes from the end of the previous scan. This process was conducted in the morning (range: 07:29–11:41) and during the afternoon (range: 14:58–19:04) for three days (total of 30 scans) to coincide with periods of high ground squirrel activity (Fitch, 1948). This process was repeated on the same days for all four plots at a given site, and the order that counts were conducted for a given site was consistent throughout. All field personnel were trained in this process before the initiation of the field study, and the same observer conducted all visual counts for a given site (4 total observers for the project). We used the maximum number of ground squirrels observed for each plot to represent ground squirrel abundance for that site, and included that value in subsequent analyses. The counts occurred from 11 May–23 June 2019 and 5 May–13 June 2020 to coincide with the period when grasses and forbs senesce at these rangeland sites. All aspects of this project pertaining to animal use were approved by the University of California, Davis' Institutional Animal Care and Use Committee (protocol no. 21063).

Estimation of standing crop

We used the comparative yield method to estimate forage standing crop for each of our study plots (Haydock and Shaw, 1975). Following George et al. (2006), we used 0.09 m^2 metal frames to identify quadrats that represented standing crop in five ranks with 1 equivalent to low standing crop and 5 indicating the highest standing crop value in the plot. When establishing these reference quadrats, we did not consider forage items that would not regularly be consumed by ground squirrels (e.g., woody plants and thistles). We placed three frames in each of the five ranks. Prior to sampling, the observer reviewed each quadrat ranking until they were confident in placing subsequent samples into their respective rank category. After visual calibration, three samples of each rank (1–5; 15 samples total) were clipped for later regression analyses. Sample collection included all current year herbaceous vegetation that would generally be consumed by ground squirrels within each frame, being careful not to include litter. All clipped vegetation was placed into individually labeled brown paper bags for drying and weighing in the lab. Individual clipping and subsequent regression equations were developed for each site unless those on a single ranch were collected the same day and were homogenous in herbaceous cover.

Following completion of this calibration period, we established a 10 × 10 grid of sampling locations within each plot (i.e., 100 total samples; Fig. 2). Each line of the grid represented a transect, with the start of the first transect located 4.4 m from the edge of the plot. Sampling points were then established in a linear line approximately 5.8 m apart. At each sampling point, we placed a 0.09 m^2 metal frame and assigned a standing crop value rank between 0 and 5. If a quadrat fell on an area of bare soil, it received a score of 0, and if the observer felt the quadrat was representative of a standing crop value that was intermediate between two ranks, we used half ranks (e.g., 0.5, 1.5, etc.). This allowed us to systematically sample throughout the entire study plot. All observers received training on this process at the start of the project, and the same individual provided ranks for each plot at a given site to reduce user bias.

Forage clippings were dried in an oven at 60–65º C for 48 hours to remove all moisture. We weighed each sample with an electronic scale to the nearest 0.1 g and converted this value to kg ha^{-1}. We then regressed these biomass values on comparative yield scores to provide conversion equations for comparative yield ranks (George et al., 2006). For regression analyses, we considered linear, polynomial, exponential, and power regressions to determine which best fit the data (McDonald, 2014). The subsequent regression equations were used to estimate standing crop biomass for each comparative yield value to determine mean standing crop biomass for each plot (see Table 2 for equations and relevant statistics).

Additional variables

Precipitation and livestock grazing intensity were two variables that we felt would account for much spatial and temporal variation in residual standing crop across years. As such, we recorded precipitation data from October through May to reflect its effect on forage production. All precipitation data were collected from the closest Remote Automatic Weather Station (https://raws.dri.edu/; RAWS, Western Regional Climate Center, Desert Research Institute, Reno, NV). To assess livestock grazing intensity, we calculated Animal Unit Months (AUMs) on a per hectare basis. To calculate AUMs, we first determined the number of days and number of cattle that were grazed in the pastures where the ground squirrel plots were located during the growing season (Oct 1 through the day that forage assessments were conducted in either May or June). This value was multiplied by animal unit equivalent values as outlined by George et al. (2020), and we then divided this value by 30 days to reflect AUMs. Lastly, we divided the resultant value by the total number of hectares for each pasture to reflect AUMs on a per hectare basis.

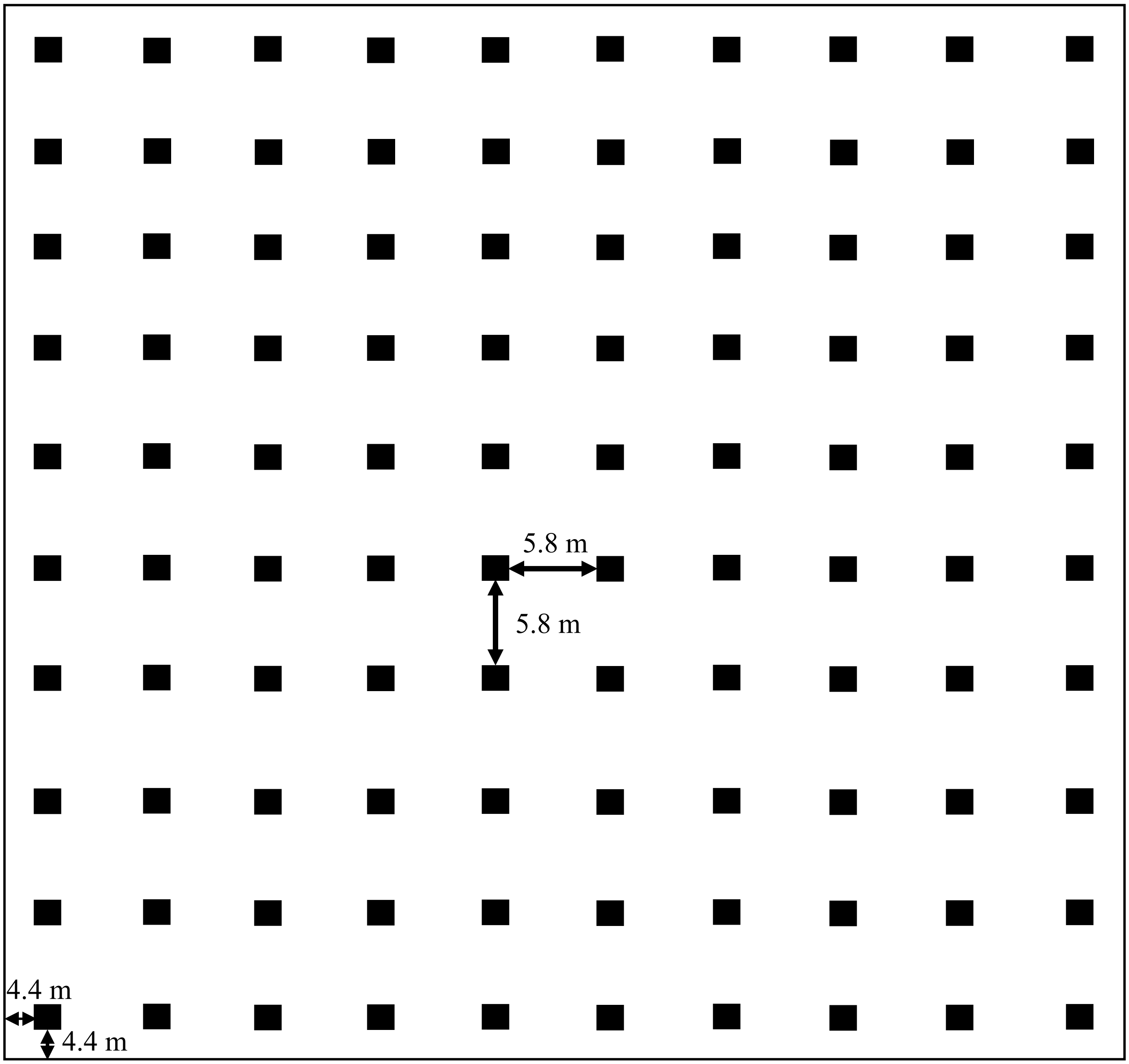

Figure 2. Example of plot layout (64 m × 64 m) illustrating how sampling locations (represented by black squares; 0.3 m in width) were distributed within each study plot. The plot contained 100 sampling locations that were used to assess residual standing crop following the comparative yield method. Outer lines of sampling locations were placed approximately 4.4 m from the edge of each plot, and the distance between each adjacent sampling location was approximately 5.8 m.

Table 2. Regression equations and corresponding R^2 values comparing comparative yield estimates (x) to estimates of standing crop biomass (y, kg ha^{-1}) in study plots corresponding to minimal, low, medium, and high ground squirrel abundance during spring 2019 and 2020 across 16 rangeland sites in California. Sites that lack regression equations were not sampled that year.

		2019		2020	
Site	GS activity	Equation	R^2	Equation	R^2
1	Minimal	$y = 86.08 - 23.88x + 126.05x^2$	0.964	$y = 248.73e^{0.546x}$	0.959
1	Low	$y = 169.83x^{1.647}$	0.934	$y = 257.07e^{0.517x}$	0.977
1	Medium	$y = 157.02x^{1.814}$	0.991	$y = 275.44e^{0.528x}$	0.931
1	High	$y = 64.45x^{2.191}$	0.974	$y = 430.68x^{0.889}$	0.928
2	Minimal	$y = 168.80x^{1.617}$	0.965	$y = 173.57e^{0.530x}$	0.958
2	Low	$y = 95.95e^{0.691x}$	0.958	$y = 324.23e^{0.478x}$	0.870
2	Medium	$y = 107.03e^{0.638x}$	0.948	$y = 1027.96 - 557.79x + 180.36x^2$	0.911
2	High	$y = 86.21e^{0.654x}$	0.976	$y = 248.00e^{0.542x}$	0.946
3	Minimal	$y = 318.50 - 221.25x + 142.44x^2$	0.996	$y = 322.09 - 8.45x + 74.04x^2$	0.933
3	Low	$y = 187.23 + 18.39x + 75.06x^2$	0.909	$y = -152.08 + 571.72x$	0.924
3	Medium	$y = 127.54x^{1.608}$	0.921	$y = 145.33e^{0.595x}$	0.970
3	High	$y = 169.13x^{1.660}$	0.920	$y = 550.20 - 174.21x + 112.73x^2$	0.902
4	Minimal	$y = 266.09e^{0.525x}$	0.908	$y = 181.49 + 58.41x + 54.83x^2$	0.915
4	Low	$y = 441.57x^{1.148}$	0.917	$y = 181.49 + 58.41x + 54.83x^2$	0.915
4	Medium	$y = 441.57x^{1.148}$	0.917	$y = 181.49 + 58.41x + 54.83x^2$	0.915
4	High	$y = 441.57x^{1.148}$	0.917	$y = 181.49 + 58.41x + 54.83x^2$	0.915
5	Minimal	$y = 513.62 - 28.80x + 181.39x^2$	0.934	$y = 27.26 + 89.31x + 69.94x^2$	0.948
5	Low	$y = 513.62 - 28.80x + 181.39x^2$	0.934	$y = 294.77x^{1.487}$	0.948
5	Medium	$y = 513.62 - 28.80x + 181.39x^2$	0.934	$y = 294.77x^{1.487}$	0.948
5	High	$y = 513.62 - 28.80x + 181.39x^2$	0.934	$y = 294.77x^{1.487}$	0.930

6	Minimal	$y = 649.22e^{0.371x}$	0.816	$y = -79.63 + 180.10x + 126.30x^2$	0.940
6	Low	$y = 649.22e^{0.371x}$	0.816	$y = 301.71x^{1.555}$	0.976
6	Medium	$y = 649.22e^{0.371x}$	0.816	$y = 301.71x^{1.555}$	0.976
6	High	$y = 550.40x^{1.288}$	0.806	$y = 301.71x^{1.555}$	0.976
7	Minimal	$y = 673.59 - 421.08x + 139.88x^2$	0.931	$y = 481.84x^{1.020}$	0.955
7	Low	$y = 749.63 - 464.28x + 148.34x^2$	0.913	$y = -151.00 + 446.55x$	0.925
7	Medium	$y = 558.81 - 203.01x + 96.84x^2$	0.850	$y = 824.23 - 96.02x + 91.21x^2$	0.897
7	High	$y = 195.78e^{0.462x}$	0.914	$y = 308.46 + 30.03x + 98.89x^2$	0.927
8	Minimal	$y = 94.39e^{0.604x}$	0.831		
8	Low	$y = 82.04e^{0.664x}$	0.979		
8	Medium	$y = 129.76e^{0.579x}$	0.964		
8	High	$y = 152.89x^{1.220}$	0.829		
9	Minimal	$y = 130.67e^{0.563x}$	0.919	$y = 197.99 - 183.64x + 125.54x^2$	0.974
9	Low	$y = 274.03 - 266.34x + 129.63x^2$	0.952	$y = 601.85 - 407.35x + 134.25x^2$	0.902
9	Medium	$y = 67.74e^{0.707x}$	0.974	$y = 95.98e^{0.616x}$	0.902
9	High	$y = 123.24x^{1.610}$	0.951	$y = 95.65e^{0.587x}$	0.936
10	Minimal	$y = 578.14e^{0.337x}$	0.758	$y = -246.41 + 632.34x$	0.941
10	Low	$y = 258.90x^{1.564}$	0.891	$y = 488.51 + 548.77x$	0.793
10	Medium	$y = 238.16 - 230.93x + 122.72x^2$	0.941	$y = 172.16 + 503.58x$	0.730
10	High	$y = 478.47 - 117.13x + 111.70x^2$	0.834	$y = 298.17x^{1.544}$	0.785
11	Minimal	$y = 2591.05 - 1607.40x + 426.31x^2$	0.872	$y = 751.06 - 269.67x + 176.52x^2$	0.831
11	Low	$y = 124.58e^{0.663x}$	0.959	$y = 96.34x^{1.952}$	0.888
11	Medium	$y = 787.49x^{1.018}$	0.820	$y = 239.98x^{1.642}$	0.875
11	High	$y = 179.42e^{0.578x}$	0.969	$y = 596.11 - 486.31x + 180.10x^2$	0.873

12	Minimal	$y = 243.18 - 231.04x + 85.31x^2$	0.967		
12	Low	$y = 239.26x^{1.224}$	0.906		
12	Medium	$y = 158.53 - 17.11x + 80.45x^2$	0.933		
12	High	$y = 205.88 - 233.19x + 99.66x^2$	0.976		
13	Minimal			$y = 44.64e^{0.784x}$	0.950
13	Low			$y = -56.67 + 49.29x + 79.42x^2$	0.983
13	Medium			$y = 54.17e^{0.783x}$	0.941
13	High			$y = 94.21x^{1.956}$	0.955
14	Minimal			$y = 226.25 - 251.23x + 166.55x^2$	0.964
14	Low			$y = 226.25 - 251.23x + 166.55x^2$	0.964
14	Medium			$y = 226.25 - 251.23x + 166.55x^2$	0.964
14	High			$y = 226.25 - 251.23x + 166.55x^2$	0.964
15	Minimal			$y = 153.15e^{0.596x}$	0.976
15	Low			$y = 153.15e^{0.596x}$	0.976
15	Medium			$y = 153.15e^{0.596x}$	0.976
15	High			$y = 153.15e^{0.596x}$	0.976
16	Minimal			$y = 905.15 - 796.98x + 266.78x^2$	0.965
16	Low			$y = 905.15 - 796.98x + 266.78x^2$	0.965
16	Medium			$y = 905.15 - 796.98x + 266.78x^2$	0.965
16	High			$y = 905.15 - 796.98x + 266.78x^2$	0.965

[a] All equations were significant a $P < 0.001$.

Statistical analysis

We used multiple linear regression to estimate standing crop (dependent variable) based on ground squirrel abundance (independent variable; McDonald, 2014). We included site as a random effect to account for potential differences across sites. We also included precipitation and AUMs as independent variables to help account for the potential effect of precipitation and livestock grazing intensity on residual standing crop. Lastly, we included the interaction between precipitation and ground squirrel abundance and the interaction between livestock grazing intensity and ground squirrel abundance to assess any interactive relationship between these variables. We initially included year as an independent variable in the model as well, but the Variance Inflation Factor for year and precipitation indicated substantial collinearity, so we removed year from further analyses as we considered precipitation the more meaningful variable. We checked for normality of residuals using the Shapiro-Wilk test (Shapiro and Wilk, 1965), and we tested for homogeneity of variance using the White test (White, 1980). We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and the difference in AIC_c (ΔAIC_c) to compare models, and we considered those models with $\Delta AIC_c < 2$ as having strong support (Burnham and Anderson 2002). All analyses were conducted using SAS (Version 9.4; SAS Institute Inc., Cary, North Carolina, USA).

RESULTS

The number of ground squirrels observed per study plot ranged from 0–30, and in general, we achieved our target numbers for minimal to high-density plots (Table 1). Total precipitation during the growing season was greater during 2019 ($\bar{x} = 49$ cm, SE = 4) than 2020 ($\bar{x} = 28$ cm, SE = 2) across all sites, yielding greater standing crop biomass during 2019 ($\bar{x} = 1{,}381$ kg ha^{-1}, SE = 111) than in 2020 ($\bar{x} = 1{,}198$ kg ha^{-1}, SE = 72; Table 1). Standing crop biomass varied substantially across sites, with the lightest biomass (232 kg ha^{-1}) reported at the high-density ground squirrel plot ($n = 22$ ground squirrels) at Site 4 during 2020 (dry year—16.7 cm precipitation), while the heaviest standing crop biomass (3,492 kg ha^{-1}) was reported at the minimal-density ground squirrel plot ($n = 1$ ground squirrel) at Site 11 during 2019 (wet year—44.6 cm precipitation; Table 1). We were able to obtain livestock grazing intensity data for most sites and years, but we lacked data for Sites 9 and 10 for both years. Animal Unit Months ha^{-1} varied considerably across sites and seasons (range = 0.37–10.53; Table 1).

Our top model included site, precipitation, ground squirrel abundance, and livestock grazing intensity (Table 3). However, livestock grazing intensity did not have a substantial effect on residual standing crop ($t = 0.5$, $P = 0.599$; Table 4). Furthermore, as previously stated, we were not able to collect information on livestock grazing intensity for two study sites (Table 1), which reduced our sample sizes when including this variable in analyses. For these reasons, we reran the models without livestock grazing intensity. Our subsequent top model indicated that site, precipitation, and ground squirrel abundance all affected forage production (Table 3). Forage production increased by 16.6 kg ha^{-1} (SE = 3.8) for every 1 cm of additional precipitation, while each additional ground squirrel located in our study plots resulted in a decrease of 27.2 kg ha^{-1} (SE = 6.6) of forage (Table 4). No other models were comparatively close ($\Delta AIC_c \geq 18.27$; Table 3).

Table 3. Resultant top models when comparing site, precipitation amount (Precip), California ground squirrel abundance (GS_count), and livestock grazing intensity (LGI) to residual standing crop across 16 rangeland sites located in the central portion of California during late spring 2019–2020. Models include the full list of variables that included LGI, as well as a reduced model that excluded LGI given the insignificance of this variable combined with a larger sample size when eliminating LGI. Model support was ranked by Akaike's Information Criterion values corrected for small sample sizes (AIC_c) and the difference in AIC_c (ΔAIC_c), with only models shown with ΔAIC_c <20.

Model	**Variables**	**No. Parameters**	**AIC_c**	**ΔAIC_c**
Full[1]	Site, Precip, GS_count, LGI	17	1160.24	
	Site, Precip, GS_count	16	1167.36	7.12
	Site, Precip, LGI	16	1174.56	14.32
	Site, Precip, LGI × GS_count	16	1179.46	19.22
	Site, GS_count, LGI	16	1180.06	19.82
Reduced[2]	Site, Precip, GS_count	18	1385.45	
	Site, Precip	17	1403.72	18.27
	Site, GS_count	17	1404.12	18.67

[1] Full model included sampling across 88 study plots. Fewer plots were included given a lack of LGI data for some of the study sites.

[2] Reduced model included sampling across 104 study plots.

Table 4. Results of top-ranked multiple linear regression models comparing site location, the amount of precipitation (Precip; cm) that fell over the forage growing season, California ground squirrel abundance (GS_count; number of ground squirrels ha^{-1}), and livestock grazing intensity (LGI; animal unit months ha^{-1}) to residual standing crop (kg ha^{-1}) at the end of the growing season across 16 rangeland sites in central California, 2019–2020. Models include the full list of variables that included LGI, as well as a reduced model that excluded LGI given the insignificance of this variable combined with a larger sample size when eliminating LGI.

	Model statistics			**Independent variable statistics**				
Model	***F***	***p***	***r*²**	**Variable**	***t***	***p***	**β**	**SE**
Full[1]	7.0	<0.001	0.61	Site[3]	2.6	<0.001		
				Precip	4.5	<0.001	19.19	4.24
				GS_count	-3.5	<0.001	-25.29	7.17
				LGI	0.5	0.599	29.84	56.46
Reduced[2]	7.9	<0.001	0.61	Site[3]	2.7	<0.001		
				Precip	4.3	<0.001	16.61	3.84
				GS_count	-4.1	<0.001	-27.15	6.60

[1] Full model included sampling across 88 study plots. Fewer plots were included given a lack of LGI data for some of the study sites.

[2] Reduced model included sampling across 104 study plots.

[3] We did not include β and associated standard errors for Site in this Table given that this is a random effect categorical variable whose values are not transferable to other potential sites. We included this variable in our models to account for variability in residual standing crop likely caused by many biotic and abiotic factors across our study sites.

DISCUSSION

California grounds squirrels are known to cause substantial forage losses in rangelands (Marsh, 1998; Fleming et al., 2013; Baldwin et al., 2014), but few quantitative assessments of these losses have been conducted. The only directly comparable study to ours was published >70 years ago. In this study, Fitch and Bentley (1949) estimated forage losses of 41.4 kg ha^{-1} per ground squirrel over a single 0.2 ha plot. The authors suggested this value might be a bit high relative to many rangelands as the plot was ungrazed by livestock and other wildlife species. Furthermore, Lidicker (1989) reassessed Fitch and Bentley's (1949) data several decades later and suggested the actual value may be closer to 23.7 kg ha^{-1} per ground squirrel. Our results are close to this value (27.2 kg ha^{-1}), which, along with the large number of study sites used within this project, provides strong support for our estimate.

The extent of forage loss caused by ground squirrels for ranchers will depend on ground squirrel abundance in a given area. Given resource limitations, we were not able to calculate ground squirrel densities for our study plots, but rather calculated a minimum number known estimate within our study plots to use an as index of ground squirrel abundance (Baldwin et al., 2021b). This approach is easily replicated and should be useful to ranchers for determining potential impacts of ground squirrels in moderate to high-abundance areas. For example, a count of 5 ground squirrels ha^{-1} would roughly equate to a loss of 136 kg ha^{-1} of forage at the end of the growing season. Conversely, a count of 75 ground squirrels ha^{-1} (equivalent to 30 per 0.4 ha which was the highest number we observed in this study) would equate to a loss of 2,040 kg ha^{-1}. Given that a cow/calf pair will consume around 425 kg mo^{-1} (George et al., 2020), these losses can be substantial. Furthermore, reductions in standing crop only account for the difference in forage availability at the end of the growing season. Ground squirrels consume and remove forage that regrows throughout the growing season. Although we do not know what this amount of forage removal is, it would further reduce the forage that is available for livestock consumption. Therefore, our use of standing crop at the end of the growing season provides a conservative estimate of forage loss; this should be considered when deciding on the need for management actions on a given ranch.

Not surprisingly, precipitation had a substantial effect on residual standing crop across the range of values observed in our study (range = 16.7–78.8 cm), as rainfall is an important driver of grassland production (George et al., 2020; Liu et al., 2022). Others have suggested that forage losses caused by ground squirrels could be exacerbated during dry years (Marsh, 1998), but we did not note an interaction between the impact that precipitation and ground squirrel abundance have on standing crop, suggesting that the proportion of available forage removed by ground squirrels will not vary substantially across the precipitation levels we observed. That said, the fact that forage production is substantially less during years with lower precipitation amounts indicates that forage losses from ground squirrels are likely more acute during drought years given less available forage overall. As such, ground squirrel management may be more cost effective during drought years. This may be a particularly important consideration over the next several decades given expected drier conditions across many California rangelands (Yoon et al., 2015; Liu et al., 2022).

Although livestock grazing certainly influences forage production and late-season standing crop values (Fehmi et al., 2005; George et al., 2020), we did not observe any impact of livestock grazing intensity on available forage. It should be pointed out that our assessment of grazing intensity was necessarily determined at a pasture level, as we had no control over stocking rates or cattle distribution throughout the ranches. Therefore, this variable may have lacked the ability to accurately track uneven grazing intensity within a pasture, potentially making it an insensitive variable for estimating residual standing crop. A more granular assessment of grazing intensity (e.g., impact of grazing only within study plots) may have yielded a different result. That said, our study was designed to provide a practical assessment of how ground squirrels affect residual standing crop at a broad pasture scale (i.e., how a rancher or land manager could use this information to estimate standing crop loss due to ground squirrels at the end of the growing season). Therefore, our results translate well to functional grazing programs.

We also did not observe a significant interaction between grazing intensity and ground squirrel abundance. This is in contrast to Fehmi et al. (2005) in that they noted that standing crop was negatively associated with ground squirrel abundance in the presence of livestock grazing. Reasons for this disparity are unclear. As previously pointed out, our assessment of grazing intensity may not have accurately captured this variable across all study plots. Additionally, Fehmi et al. (2005) only used low to moderate grazing intensities in their study, and they noted that more intensive grazing pressure might yield different results. Our investigation utilized a wide range of grazing intensities, including more heavily grazed rangelands (range = 0.37–10.53 AUMs ha^{-1}). Likewise, our study sites represented a much broader swath of locations with varying levels of forage production when compared to Fehmi et al. (2005). This introduced further unexplained variability in the models, but also allowed for a more robust assessment of forage removal by ground squirrels by testing across a larger range of biotic and abiotic factors. Ultimately, the disparity in results from these two studies likely reflects the complicated relationship between livestock grazing intensity and ground squirrel abundance, and their collective influence on residual standing crop may require further investigation.

It bears noting that we only assessed ground squirrel damage via a reduction in residual forage. Ground squirrels can damage ranching operations in a variety of ways. For example, the construction of burrow systems undermines ranch roads, pond dams, and levees (Marsh, 1998; Van Vuren et al., 2014; Wolf et al., 2017), leading to expensive repair costs or potential catastrophic damage from a dam or levee failure (Fitzgerald and Marsh, 1986; Bayoumi and Meguid, 2011). Burrows can also lead to hill slumping and other forms of soil erosion when water from heavy rainfall events channels through the burrow systems (Longhurst, 1957). Furthermore, burrow entrances pose a tripping hazard for livestock, potentially leading to broken legs and subsequent mortality (Marsh, 1998; Weir et al., 2016). The economic impact of these types of damage have not been accurately assessed in California rangelands and merits investigation.

Although California ground squirrels can cause substantial damage in rangelands, it is important to note that they can also serve an important ecological role as ecosystem engineers. Their burrow systems provide habitat for numerous species including burrowing owls (*Athene cunicularia hypugaea*), California tiger salamanders (*Ambystoma californiense*), and San Joaquin kit foxes (*Vulpes macrotis mutica*) (Fitch, 1948; Loredo et al., 1996; Warrick et al., 2007), and native bird species richness, diversity, and abundance has been documented to be greater around ground squirrel colonies (Lenihan, 2007). Furthermore, the presence of

California ground squirrels has been postulated to increase soil fertility and subsequent plant production (Lidicker, 1989), although a rigorous assessment of this assertion has not yet been conducted. Clearly, California ground squirrels are an important part of California rangelands and should be conserved when they are not causing deleterious effects to these rangeland ecosystems. The results presented from this research can help individual range managers determine their specific threshold for balancing these benefits with those of lost forage production so site-specific management programs can be determined.

MANAGEMENT IMPLICATIONS

When present in moderate to high numbers, California ground squirrels can substantially reduce standing crop in California rangelands. However, this loss in forage, combined with damage to ranch infrastructure, rangeland erosion, and potential livestock injury associated with ground squirrel burrow systems, should be weighed against the cost of management actions and the potential benefits that ground squirrels provide to grassland ecosystems when considering the need for ground squirrel management. This study provides an initial step toward understanding economic damage caused by California ground squirrels to ranchers. Future investigations should focus on economic losses associated with ground squirrel burrow systems, as well as financial costs associated with management programs to determine when ground squirrel management will be cost effective. This has particular relevance when considering management actions on public versus private lands given variable management costs depending on how much of the expense of ground squirrel control is borne by the rancher versus taxpayers; there may be less incentive to reduce ground squirrel numbers in lower density populations if the full management cost is borne by the rancher. Collectively, information about ground squirrel damage and associated management costs would allow for the development of an Integrated Pest Management program for ground squirrels in rangelands, ultimately allowing for cost effective and efficacious management of this burrowing rodent (Sterner, 2008; Fleming et al., 2013; Baldwin et al., 2014).

ACKNOWLEDGMENTS

We thank numerous ranchers for providing access to their property for this project. We also thank L. Macaulay for initial discussions on this project, and to J. Bartolome for providing helpful comments on this manuscript. This work was supported by the Vertebrate Pest Control Research Advisory Committee of the California Department of Food and Agriculture (grant number 18-00488-000-SA), and the University of California's Division of Agriculture and Natural Resources.

LITERATURE CITED

Baldwin, R.A., Becchetti, T.A., Meinerz, R., Quinn, N., 2021a. Potential impact of diphacinone application strategies on secondary exposure risk in a common rodent pest: implications for management of California ground squirrels. Environmental Science and Pollution Research 28, 45891–45902.

Baldwin, R.A., Becchetti, T.A., Quinn, N., Meinerz, R., 2021b. Utility of visual counts for determining efficacy of management tools for California ground squirrels. Human-Wildlife Interactions 15, 138–147.

Baldwin, R.A., Salmon, T.P., Schmidt, R.H., Timm, R.M., 2014. Perceived damage and areas of needed research for wildlife pests of California agriculture. Integrated Zoology 9, 265–279.

Bayoumi, A., Meguid, M.A., 2011. Wildlife and safety of earthen structures: a review. Journal of Failure Analysis and Prevention 11, 295–319.

Boellstorff, D.E., Owings, D.H., 1995. Home range, population structure, and spatial organization of California ground squirrels. Journal of Mammalogy 76, 551–561.

Brunson, M.W., Huntsinger, L., 2008. Ranching as a conservation strategy: can old ranchers save the new west? Rangeland Ecology and Management 61, 137–147.

Burnham, K.P, Anderson, D.R., 2002. Model selection and inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, NY, USA, p. 488.

Fehmi, J.S., Russo, S.E., Bartolome, J.W., 2005. The effects of livestock on California ground squirrels (*Spermophilus beecheyi*). Rangeland Ecology and Management 58, 352–359.

Fitch, H.S., 1948. Ecology of the California ground squirrel on grazing lands. American Midland Naturalist 39, 513–596.

Fitch, H.S., Bentley, J.R., 1949. Use of California annual-plant forage by range rodents. Ecology 30, 306–321.

Fitzgerald, W.S., Marsh, R.E., 1986. Potential of vegetation management for ground squirrel control. Proceedings of the Vertebrate Pest Conference 12, 102–107.

Fleming, P.J.S., Limin, H., Whisson, D., 2013. Impacts and management of invasive burrowing herbivores in grasslands. Proceedings of the International Grassland Congress 22, 1600–1608.

George, M.R., Barry, S.J., Larson, S.R., McDougald, N.K., Ward, T.A., Harper, J.M., Dudley, D.M., Ingram, R.S., Laca, E.A., 2006. Comparison of comparative yield and stubble height for estimating herbage standing crop in annual rangelands. Rangeland Ecology and Management 59, 438–441.

George, M., Frost, W., McDougald, N., 2020. Ecology and management of annual rangelands series: grazing management. University of California Division of Agriculture and Natural Resources Publication 8547.

Grinnell, J., Dixon, J., 1918. Natural history of the ground squirrels of California. California State Commission of Horticulture Monthly Bulletin 7, 597–708.

Haydock, K.P., Shaw, N.H., 1975. The comparative yield method for estimating dry matter yield of pasture. Australian Journal of Experimental Agriculture and Animal Husbandry 15, 663–670.

Hindmarch, S., J. E. Elliott, J.E., 2018. Ecological factors driving uptake of anticoagulant rodenticides in predators. In: van den Brink, N.W., Elliott, J.E., Shore, J.E., Rattner, J.R. (Eds.), Anticoagulant rodenticides and wildlife. Springer International Publishing, Cham, Switzerland, pp. 229–258.

Howard, W.E., Wagnon, K.A., Bentley, J.R., 1959. Competition between ground squirrels and cattle for range forage. Journal of Range Management 12, 110–115.

Huntsinger, L., Bartolome, J., D'Antonio, C., 2007. Grazing on California's Mediterranean grasslands. In: Stromberg, M., Corbin, J., D'Antonio, C. (Eds.), Grazing management on California's Mediterranean grasslands. University of California Press, Berkeley, CA, USA, pp. 233–253.

Koprowski, J.L., Goldstein, E.A., Bennett, K.R., Pereira Mendes, C., 2016. Family Sciuridae (tree, flying and ground squirrels, chipmunks, marmots and prairie dogs). In: Wilson, D.E., Lacher, T.E., Jr., Mittermeier, R.A. (Eds.), Handbook of the Mammals of the World, Vol 6, Lagomorphs and Rodents 1. Lynx Edicions, Barcelona, Spain, pp. 648–837.

Larsen, R.E., Horney, M.R., Macon, D., 2014. Update of the 2014 drought on California rangelands. Rangelands 36, 52–58.

Lenihan, C.M., 2007. The ecological role of the California ground squirrel (*Spermophilus beecheyi*). Dissertation, University of California, Davis, USA, pp. 107.

Li, G., Liu, Y., Frelich, L.E., Sun, S., 2011. Experimental warming induces degradation of a Tibetan alpine meadow through trophic interactions. Journal of Applied Ecology 48, 659–667.

Li, G., Yin, B., Wan, X., Wei, W., Wang, G., Krebs, C.J., Zhang, Z., 2016. Successive sheep grazing reduces population density of Brandt's voles in steppe grassland by altering food resources: a large manipulative experiment. Oecologia 180, 149–159.

Lidicker, W.Z., Jr., 1989. Impacts of non-domesticated vertebrates on California grasslands. In: Huenneke, L.F., Mooney, H. (Eds.), Grassland structure and function: California annual grassland. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 135–150.

Lipiec, J., Doussan, C., Nosalewicz, A., Kondracka, K., 2013. Effect of drought and heat stresses on plant growth and yield: a review. International Agrophysics 27:463–477.

Liu, H., Jin, Y., Roche, L.M., O'Geen, A.T., Dahlgren, R.A., 2022. Impacts of climate change on California's rangeland production: sensitivity and future projection. bioRxiv doi: https://doi.org/10.1101/2022.02.06.479265.

Longhurst, W.M., 1957. A history of squirrel burrow gully formation in relation to grazing. Journal of Range Management 10, 182–184.

Loredo, I., Van Vuren, D., Morrison, M.L., 1996. Habitat use and migration behavior of the California tiger salamander. Journal of Herpetology 30, 282–285.

Marsh, R.E., 1998. Historical review of ground squirrel crop damage in California. International Biodeterioration and Biodegradation 42, 93–99.

McDonald, J.H., 2014. Handbook of biological statistics, 3rd edition. Sparky House Publishing, Baltimore, MD, USA, p. 299.

Quinn, N.M., Dimson, M.J., Baldwin, R.A., 2018. Pest Notes: Ground squirrels. University of California Statewide Integrated Pest Management Program, Division of Agriculture and Natural Resources, Publication 7438.

Rattner, B.A., Lazarus, R.S., Elliott, J.E., Shore, R.F., van den Brink. N., 2014. Adverse outcome pathway and risks of anticoagulant rodenticides to predatory wildlife. Environmental Science & Technology 48, 8433–8445.

Schieltz, J.M., Rubenstein, D.I., 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? Environmental Research Letters 11, 113003.

Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.

Sterner, R.T., 2008. The IPM paradigm: vertebrates, economics, and uncertainty. Proceedings of the Vertebrate Pest Conference 23, 194–200.

Van Vuren, D.H., Ordeñana, M.A., McGrann, M.C., Berentsen, A.R., 2014. Managing California ground squirrels on levees using habitat modification. Proceedings of the Vertebrate Pest Conference 26, 180–183.

Warrick, G.D., Clark, H.O., Kelly, P.A., Williams, D.F., Cypher, B.L., 2007. Use of agricultural lands by San Joaquin kit foxes. Western North American Naturalist 67, 270–277.

Weir, R.D., Davis, H., Gayton, D.V., Lofroth, E.C., 2016. Fact or fantasy? Damage to livestock and agricultural machinery by American badgers and other burrowing mammals in British Columbia, Canada. In: Proulx, G., Do Lihn San, E. (Eds.), Badgers: systematics, biology, conservation and research techniques. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada, pp. 299–310.

White, H., 1980. A heteroscedasticity-consistent covariance matrix estimator and a direct test for heteroscedasticity. Econometrics 48, 817–838.

Wolf, K.M., Baldwin, R.A., Barry, S., 2017. Compatibility of livestock grazing and recreational use on coastal California public lands: importance, interactions, and management solutions. Rangeland Ecology & Management 70, 192–201.

Wolf, K.M., Whalen, M.A., Bourbour, R.P., Baldwin, R.A., 2018. Rodent, snake and raptor use of restored native perennial grasslands is lower than use of unrestored exotic annual grasslands. Journal of Applied Ecology 55, 1133–1144.

Yoon, J., Wang, S., Gillies, R.R., Kravitz, B., Hipps, L., Rasch, P.J., 2015. Increasing water cycle extremes in California and in relation to Enso cycle under global warming. Nature Communications 6, 8657.

Zhang, J., Li, J., Xiao, R., Zhang, J., Wang, D., Miao, R., Song, H., Liu, Y., Yang, Z., Liu, M., 2020. The response of productivity and its sensitivity to changes in precipitation: a meta-analysis of field manipulation experiments. Journal of Vegetation Science 32, e12954.